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Optimal harvest of age-structured populations of moose *Alces alces* in a fluctuating environment

Bernt-Erik Sæther, Steinar Engen & Erling J. Solberg

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We analysed sex- and age-specific harvesting strategies of moose using an age-structured population model that includes density dependence as well as environmental stochasticity. In order to find the strategy that maximises the mean annual yield we simulated the process over a large number of years. The mean annual yield is a function of the three parameters (number of harvested individuals of calves, adult ($\geq 1\frac{1}{2}$ years old) bulls and adult females) that are involved in the definitions of the strategies. We compare, by numerical maximisation of a function in several variables, two harvest strategies: proportional harvesting, i.e. removal of a certain proportion of individuals in a given age- and sex-class, and threshold harvesting, i.e. all individuals of a given sex- and age-class are harvested when the size of this subpopulation exceeds a certain threshold. In general, proportional harvest gives a smaller mean annual yield than threshold harvesting. The variance in the annual yield is, however, larger for threshold than for proportional harvesting. These differences between the two harvest strategies increase when the annual survival of calves is low, when there is high environmental stochasticity and when there is strong density regulation operating on survival. For both harvest strategies, the optimal harvest strategy involves high harvest of calves and adult bulls, whereas adult females should hardly be harvested.

Key words: age-specific harvesting, density dependence, environmental stochasticity, moose, stochastic population dynamics

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Most populations fluctuate, and coefficients of variation of 20-80% are commonly found in many vertebrate species (Pimm 1991, B-E. Sæther & S. Engen, unpubl. data). Most of this variation is caused by stochastic variation in the environment that can not be accounted for in traditional deterministic population models. Thus, harvesting principles such as maximum sustainable yield derived from analyses of such models will therefore not

be able to include important components of the dynamics of most harvested populations.

Using general diffusion theory, Lande, Engen & Sæther (1995) and Lande, Sæther & Engen (1997) compared different harvesting strategies in a fluctuating environment without requiring stationary distribution of population sizes. They found, for a variety of optimising criteria, that threshold harvesting, i.e. harvesting all indi-

viduals above a certain population size, but no harvest below that threshold, was superior to proportional harvesting, i.e. removing a certain proportion of the population, as well as to constant harvesting (i.e. removal of a constant number of individuals, irrespective of population size). These analyses were based on a number of simplifying assumptions, e.g. continuous harvest, no age-structure, unlimited harvest capacity and exactly known population sizes.

Many important harvested species are long-lived, and often possess strong age-dependent variation in demographic variables (e.g. Sæther 1997). Development of harvest strategies for such species often relies on an extensive use of simulation models (Getz & Haight 1989, Quinn & Deriso 1999). A common problem encountered by this approach is to obtain reliable estimates of essential parameters. Often this introduces serious problems when interpreting the results from such analysis, which makes it difficult to obtain robust general conclusions from this type of models.

In this paper we will examine whether the general conclusions obtained from very simplified population models also can be useful for development of harvesting strategies of populations of species with more complicated demography. We will focus our analyses on the moose *Alces alces* population in the Vefsn Valley in northern Norway which has been studied since 1967 (Sæther 1985, 1987, Solberg, Sæther, Strand & Loison 1999, Solberg, Loison, Sæther & Strand 2000). Variation in many of the demographic variables of this species is closely related to age (Sæther & Haagenrud 1983, 1985, Sæther 1987, Sæther & Heim 1993, Sand 1996a, Sæther, Andersen, Hjeljord & Heim 1996a, Solberg et al. 2000, Ericsson 1999, Stubbsj en, S  ther, Solberg, Heim & Rolandsen 2000). Thus, the effects of age-structure must be considered when deriving harvest strategies for this species. Furthermore, environmental stochasticity as well as density dependence strongly influence the population dynamics of moose (S  ther et al. 1996a, Solberg et al. 1999). Based on analyses of a complex stochastic age-structured population model we will examine how variation in different parameters affects the composition of the optimal harvest strategy. In this way we hope to present some general guidelines for the management of moose populations in a fluctuating environment.

Characteristics of the moose demography and population dynamics in Scandinavia

Over most of its distributional range in Scandinavia, moose currently encounters an environment almost

free of large predators. This implies that the survival rates in general are much higher in Scandinavia than in most North American populations (S  ther et al. 1996a, Ericsson 1999, Stubbsj en et al. 2000). As a consequence, high population growth rates are expected in populations that are not subject to hunting (S  ther 1987, Cederlund & Sand 1991). S  ther et al. (1996a) argued that a stable equilibrium between the moose and its food resources is unlikely in the absence of large predators (see Messier 1994) because the regulatory feedbacks from the vegetation become too slow.

Moose regularly produce twins (Franzman 1981), probably evolved as an adaptation to exploitation of patchily distributed food resources (Geist 1974). The twinning rate is age-dependent because young females rarely produce more than a single calf (Franzman 1981, S  ther & Haagenrud 1983, 1985, Sand 1996b). However, as is generally the case in large herbivores (S  ther 1997), size-dependent variation occurs in several reproductive traits of the moose (S  ther & Haagenrud 1985, S  ther & Heim 1993, S  ther et al. 1996a, Sand 1996b), resulting in an interaction between age and size (Caswell 2001). For instance, the probability of maturation increases with the weight of the yearling female (S  ther & Heim 1993, Sand & Cederlund 1996). Early age at maturity is in turn associated with a subsequent earlier onset of production of twin calves (S  ther & Haagenrud 1983, S  ther et al. 1996a).

Both climate and population size affect the demography through an effect on the body mass of females. High population density may lead to retarded body growth (Solberg & S  ther 1994, Solberg et al. 1999, Hjeljord & Hist  l 1999), resulting in late onset of maturation. As a consequence, the contribution to the population growth of the youngest age classes is reduced. Similarly, variation in climate may also affect the body growth of calves. Cold summers with heavy precipitation (S  ther 1985, Solberg & S  ther 1994, Sand 1996a) or mild snow-free winters (Cederlund, Sand & Pehrson 1991, S  ther et al. 1996a, Hjeljord & Hist  l 1999) are often associated with large calf weights. In addition, large annual variation is often found in neonatal calf survival in northern populations (S  ther et al. 1996a, Stubbsj en et al. 2000). Thus, environmental stochasticity should be considered when developing management strategies for moose populations.

These demographic characteristics of the moose create the potential for large fluctuations in the size of moose populations. In a long-term study in northern Norway Solberg et al. (1999) demonstrated both direct and delayed effects on the population dynamics. The delayed effects occurred mainly through changes in the age-dis-

tribution due to delays in changes in quotas in relation to variation in population size, and through stochastic variation in climate affecting the body mass of the young females and thereby the mean age at maturity.

The model

Our basis for the modelling is the moose population in 'Vefsn-dalføret' in northern Norway (see Solberg et al. 1999, 2000). We also included data from other Scandinavian populations (e.g. Sæther et al. 1996a, Stubsjøen et al. 2000) where appropriate.

We considered an age-structured population with f_i females and m_i males in age class i , $i = 0, 1, \dots$. The changes in the number of individuals from one year to the next were split up into three components, reproduction in the spring, harvesting in the autumn, and survival during the winter. At the end of the winter season all individuals were moved from one age-class to the next.

Following the available knowledge from population studies of ungulates (Sæther 1997, Gaillard, Festa-Bianchet & Yoccoz 1998, Gaillard, Festa-Bianchet, Yoccoz, Loison & Toigo 2000), we assume stochastic environmental effects affecting the reproduction of all females, as well as independent environmental effects acting on the winter survival of all individuals. Furthermore, demographic stochasticity in the reproduction is acting independently on all females, as well as demographic stochasticity in the survival modelled by binomial sampling.

Although several modifications now may exist locally, the quota system in Norway is basically based on three different age and sex categories: calves, adult ($\geq 1\frac{1}{2}$ years) females and adult males (Østgård 1987, Haagenrud, Morow, Nygren & Stålfelt 1987, Solberg et al. 1999, 2000). We consider two different harvesting strategies acting on these three different categories of the population. By proportional harvesting (Lande et al. 1995) we mean that prefixed proportions of the estimated size of each subpopulation is attempted harvested. There is also stochasticity in the harvesting modelled by assuming that each individual is then harvested independently of each other with this probability. For threshold harvesting, we define a prefixed threshold for each subpopulation. If the estimated number of individuals is above the threshold we attempt harvesting the difference between the estimate and the threshold, otherwise this subpopulation is not harvested at all. Each year, this strategy defines a proportion of each class to be harvested. Also in this case we assume that the individuals are harvested independently of each other with this probability.

Reproduction

Let r_i , $i = 2, 3, \dots$ denote the mean fecundity rate of a female of age i when the population size is so small that there is no density-regulation acting, and there is no shortage of males. Writing n for the total population size, we introduce a density-regulation by a factor $\exp(-n/n_r)$ acting only on the females in the second age-class, so that n_r is the population size at which her reproduction is a proportion $e^{-1} \approx 0.37$ of its maximum at small population sizes. Writing s for the sex-ratio between the number of reproducing females one year old or older, and the number of adult males (older than zero), we assume that the fraction of females reproducing is $1 - e^{-\alpha s}$. In most of our simulations we have chosen α so that this fraction is 0.9 when the sex ratio is $\frac{1}{3}$, that is $\alpha = 3\ln(10) \approx 6.901$. The total reproduction is then written as

$$R = \left[f_2 r_2 e^{-n/n_r} + \sqrt{f_2} \sigma_{dr} U_2 + f_2 \sigma_{er} U_{er} + \sum_{i=3}^{\infty} (f_i r_i + \sqrt{f_i} \sigma_{dr} U_i + f_i \sigma_{er} U_{er}) \right] (1 - e^{-\alpha s}).$$

The U_i and U_{er} are independent normal variates with zero means and unit variance, while σ_{dr} and σ_{er} denote components in the reproduction of the demographic and environmental stochasticity, respectively. Hence, the reproduction, R , is normal with mean

$$\bar{R} = \left[f_2 r_2 e^{-n/n_r} + \sum_{i=3}^{\infty} f_i r_i \right] (1 - e^{-\alpha s})$$

and variance

$$\text{var}(R) = (f \sigma_{dr}^2 + f^2 \sigma_{er}^2) (1 - e^{-\alpha s})^2$$

where

$$f = \sum_{i=2}^{\infty} f_i$$

is the total number of potentially reproducing females. The new-born individuals now enter age-class zero.

Harvesting

In order to simplify the notation we now redefine the f_i and m_i to be the number of individuals after reproduction. We consider the three subpopulations of sizes

$$n_0 = f_0 + m_0$$

$$n_f = \sum_{i=1}^{\infty} f_i$$

$$n_m = \sum_{i=1}^{\infty} m_i$$

and assume that there are available estimates \hat{n}_0 , \hat{n}_f and \hat{n}_m . The strategy of proportional harvesting is defined by three proportions (p_0 , p_f , p_m). When these are specified the number of individuals harvested from the zero group is binomially distributed with parameters \hat{n}_0 and p_0 , and similarly for the other two groups. Since the estimates are different from the real size of each subpopulation, the harvested amount may theoretically become larger than the size of the subpopulation, in which case we may choose the harvest to be the total subpopulation. With the parameters we have chosen in our simulations, this will never occur in practice.

Threshold harvesting differs from proportional harvesting only by the definition of the probabilities (p_0 , p_f , p_m). The probabilities are defined by three thresholds (c_0 , c_f , c_m) by choosing $p_0 = (\hat{n}_0 - c_0) / \hat{n}_0$ if $\hat{n}_0 > c_0$, and otherwise zero. The probabilities p_f and p_m are defined in the same way.

Survival

If there is no environmental stochasticity and the total population size is small we write q_i for the probability of survival of the individuals in the i^{th} age-class. Taking density-regulation and environmental stochasticity into account we use the survival probabilities of the form

$$Q_0 = q_0 \exp(-n/n_{q_0} + \sigma_{ep} U_{ep})$$

and

$$Q_i = q_i \exp(-n/n_{q_i} + \sigma_{ep} U_{ep})$$

for $i > 0$, where U_{ep} is a normal variate with zero mean and unit variance which are independent of those used to define reproduction. The parameter σ_{ep}^2 is a component of the total environmental stochasticity due to fluctuations in the winter survival, and n_{q_0} and n_{q_i} are the population sizes at which the calf survival rate and adult survival rate, respectively, is $e^{-1} \approx 0.37$ of its maximum at small population sizes.

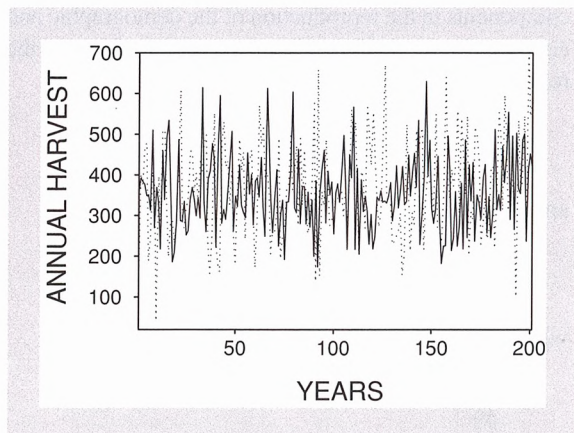


Figure 1. Annual variation during a period of 200 years in the number of animals shot of a rapidly growing moose population, harvested according to a threshold (---) or a proportional (—) strategy. The thresholds defining the optimal strategy are 353 calves, 1,425 adult ($\geq 1\frac{1}{2}$ years old) females and 296 adult males. Mean (\pm SD) population size before the harvest was $1,729 \pm 127$ individuals, whereas mean annual yield for this strategy was 368 ± 121 individuals. The optimal proportions when the population is harvested according to a proportional harvest strategy are 0.481, 0.005 and 0.182 for calves, adult females and males, respectively. Mean (\pm SD) population size before harvest was $1,549 \pm 153$ individuals, whereas mean annual yield for proportional harvest was 359 ± 89 individuals. The parameters are (see text for definitions): $q_0 = 0.80$, $q_1 = 0.90$, $q_i = 0.97$ for $2 \leq i \leq 10$, $q_{11} = 0.96$, $q_{12} = 0.94$, $q_{13} = 0.90$, $q_{14} = 0.85$, $q_{15} = 0.80$, $q_{16} = 0.70$, $q_{17} = 0.60$, $q_{18} = 0.50$, $q_{19} = 0.30$, $q_{20} = 0.10$, $r_2 = 0.22$, $r_1 = 1.30$ for $3 \leq i \leq 11$, $r_{12} = 1.20$, $r_{13} = 1.10$, $r_{14} = 1.00$, $r_{15} = 0.90$, $r_{16} = 0.80$, $r_{17} = 0.60$, $r_{18} = 0.40$, $r_{19} = 0.20$, $r_{20} = 0.10$, $n_r = 6000$, $n_{q_0} = 3000$, $n_{q_i} = 20000$ and $\sigma_{ep} = 0.04$.

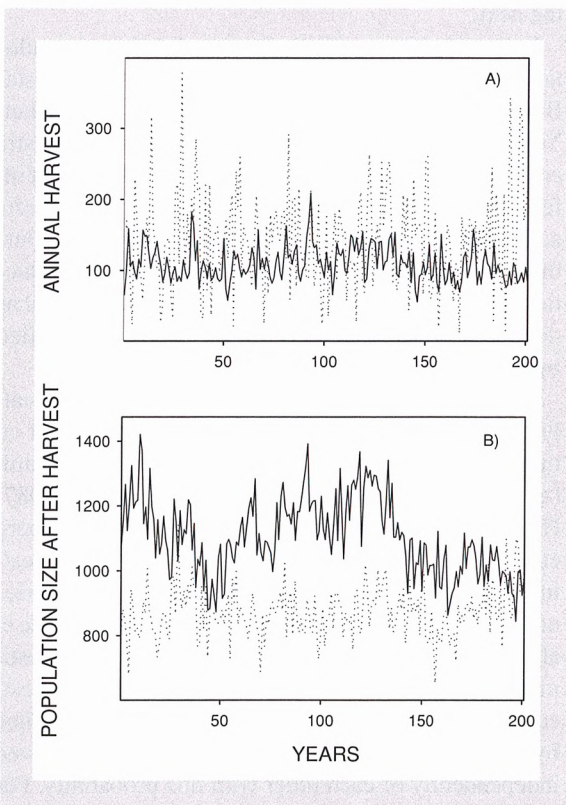


Figure 2. Annual variation during a period of 200 years in the number of animals A) remaining after the hunting season and B) the numbers harvested of a moose population with low calf survival rate ($q_0 = 0.40$), harvested according to a threshold (---) or a proportional (—) strategy. The mean (\pm SD) annual yield was 110 ± 23 and 141 ± 65 individuals for proportional and threshold harvesting, respectively. The thresholds defining the optimal strategy are 228 calves, 424 adult ($\geq 1\frac{1}{2}$ years old) females and 149 adult males. The optimal proportions when the population is harvested according to a proportional harvest strategy are 0.15, 0.01 and 0.20 for calves, adult females and males, respectively. For other parameters, see legend to Figure 1.

Numerical maximisations

Our aim is to determine the strategy among those we have selected that gives the largest mean annual yield. In order to find this strategy, we simulate the process over a large number of years. If we use a fixed seed to start the simulations of the random variables involved, then the mean annual yield is simply just a function of the three parameters involved in the definitions of the strategies for each of the two classes of strategies. The numerical maximisation can then be carried out using some standard numerical procedure for maximising functions in several variables.

Results

Optimising the mean annual yield gave large fluctuations in the number of animals that should be harvested both for proportional and threshold harvesting (Fig. 1 and 2A). In general, the variance in the mean annu-

al yield was higher for threshold than for proportional harvesting (see Fig. 1 and 2A). In contrast, population sizes after harvest were more stable when subject to threshold harvesting (see Fig. 2B).

The optimal harvest rate differed strongly among the different age- and sex-classes (Fig. 3). Calves should be subject to the most intense harvest for proportional harvesting, whereas the threshold for adult bulls was slightly lower than the calf threshold when threshold harvesting was chosen. In contrast, for both harvest strategies small quotas of adult females maximised the annual yield.

The age- and sex-specific composition of the optimal harvest strategy was strongly influenced by variation in the calf survival rate. For proportional harvesting the proportion of calves that should be removed decreased from 0.48 for a calf survival of 90% to 29% when 40% of the calves survived (see Fig. 3A). In contrast, for threshold harvesting the threshold for adult females increased strongly with calf survival rate, whereas the threshold for calves and adult males changed little (see Fig. 3B). As a consequence, the proportion of

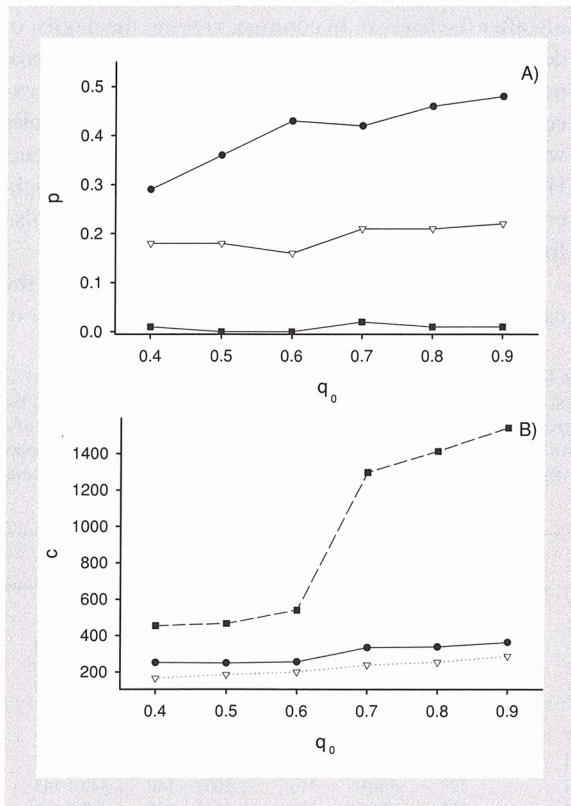


Figure 3. Proportions (p) of calves (●), adult ($\geq 1\frac{1}{2}$ years old) females (■) and adult males (▽) that maximise the annual yield of proportional harvesting (A), and the thresholds (c) of calves, adult females and adult males that maximise the annual yield of threshold harvesting (B) in relation to variation in calf survival rate q_0 . For other parameters, see legend to Figure 1. The simulations were run for 5,000 years.

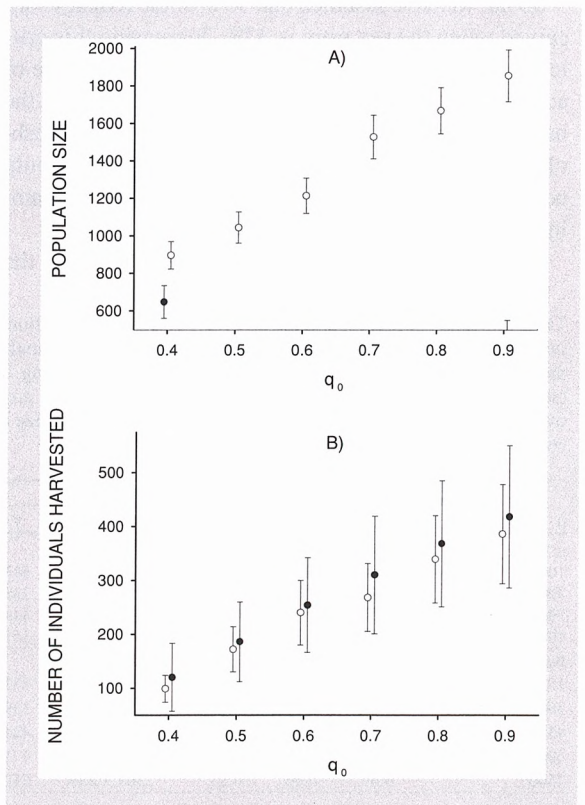


Figure 4. Mean (\pm sd) population size after harvest (A) and the mean (\pm sd) annual yield (B) in relation to variation in calf survival rate (q_0) for proportional (○) and threshold (●) harvesting during a period of 5,000 years. For other parameters, see legend to Figure 1.

Table 1. Effects of variation in the critical sex ratio, s , with a probability for a female of conceiving of 0.9, on the age- and sex-specific composition of the optimal harvest strategy, the population size remaining after harvest (\bar{x}) and the mean annual yield (\bar{y}) for proportional and threshold harvesting; p_0 , p_f and p_m are the optimal proportions to be harvested of calves, adult females and adult males, respectively, and c_0 , c_f and c_m are the optimal threshold population size of calves, adult females and adult males, respectively. For other parameters, see legend to Figure 1.

s	Proportional harvesting					Threshold harvesting				
	p_0	p_f	p_m	$\bar{x} \pm \text{sd}$	$\bar{y} \pm \text{sd}$	c_0	c_f	c_m	$\bar{x} \pm \text{sd}$	$\bar{y} \pm \text{sd}$
0.3	0.44	0.01	0.23	1623 \pm 157	325 \pm 73	326	1403	223	1629 \pm 128	348 \pm 110
0.4	0.44	0.02	0.19	1494 \pm 147	288 \pm 66	329	1371	309	1661 \pm 121	315 \pm 105
0.5	0.47	0.00	0.11	1574 \pm 161	282 \pm 72	295	1279	325	1573 \pm 114	294 \pm 97

calves and bulls removed increased, but the proportion of adult females removed decreased strongly with increasing calf survival rate. For both harvest strategies, an increase in calf survival increased both the mean population size after harvest and the mean annual yield (Fig. 4). A comparison between threshold harvesting and proportional harvesting showed that the relative difference between the two harvesting strategies was reduced with increasing calf survival (see Fig. 1, 2 and 4B). At low calf survival rates, threshold harvesting gave a relatively higher yield, but with a larger variance, than proportional harvesting.

So far, we have assumed that 90% of the females conceived when the sex ratio is 33%. Increasing this critical sex ratio reduces the yield and the harvest rate of adult bulls for both strategies (Table 1). In contrast, the harvest rate of calves is increased, especially for threshold harvesting. Low harvest of adult females should occur even when assuming an even sex ratio for obtaining a 90% probability of conception.

Varying the strength of density dependence in the

fecundity rate did not influence the age- and sex-specific composition of the optimal harvest strategy neither for threshold nor proportional harvesting (Table 2). A larger effect on the yield occurred for proportional than for threshold harvesting.

Varying the strength of density regulation in mortality strongly influenced the age- and sex-specific composition of the optimal threshold harvesting strategy (see Table 2). When the density regulation in the calf or adult survival rate is reduced, all three thresholds increase, resulting in higher yields and larger populations remaining after the harvest. In contrast, varying the degree of density regulation did not influence the optimal proportional harvest strategy (see Table 2). The only exception is a slight increase in the proportion of adult males with decreasing density regulation in the calf survival rate. However, larger post-harvest population sizes and higher yields occur with decreasing density regulation also for proportional harvest.

Increasing the environmental stochasticity in the calf survival rate reduced the yield and the number of

Table 2. Effects of variation in the strengths of density regulation in the fecundity rate (n_f), in calf survival rate (n_{q0}) and in adult survival rate (n_{qi}) on the age- and sex-specific composition of the optimal harvest strategy, the population size remaining after harvest (\bar{x}) and the mean annual yield (\bar{y}) for proportional and threshold harvesting. The strength of density regulation decreases with increasing values of n (see text for further explanation); p_0 , p_f and p_m are the optimal proportion to be harvested of calves, adult females and adult males, respectively, and c_0 , c_f and c_m are the optimal threshold population size of calves, adult females and adult males, respectively. For other parameters, see legend to Figure 1.

n	Proportional harvesting					Threshold harvesting				
	p_0	p_f	p_m	$\bar{x} \pm \text{sd}$	$\bar{y} \pm \text{sd}$	c_0	c_f	c_m	$\bar{x} \pm \text{sd}$	$\bar{y} \pm \text{sd}$
$n_f =$										
1000	0.44	0.01	0.20	1575 \pm 160	343 \pm 84	336	1427	276	1668 \pm 126	358 \pm 121
3000	0.44	0.01	0.19	1592 \pm 154	338 \pm 79	325	1397	261	1638 \pm 125	363 \pm 120
5000	0.47	0.01	0.20	1538 \pm 161	344 \pm 83	341	876	265	1678 \pm 125	366 \pm 120
10000	0.44	0.01	0.20	1659 \pm 159	351 \pm 82	329	1387	260	1643 \pm 123	364 \pm 119
$n_{q0} =$										
1500	0.47	0.00	0.17	1072 \pm 105	233 \pm 57	209	876	159	1057 \pm 84	241 \pm 79
3000	0.46	0.01	0.21	1528 \pm 160	339 \pm 81	339	1414	254	1668 \pm 123	368 \pm 117
4500	0.46	0.01	0.18	1981 \pm 192	424 \pm 101	398	1693	316	2002 \pm 149	442 \pm 143
6000	0.43	0.00	0.21	2298 \pm 216	471 \pm 111	470	1917	369	2313 \pm 166	498 \pm 160
7500	0.45	0.00	0.21	2307 \pm 239	510 \pm 119	482	2063	379	2427 \pm 176	535 \pm 171
$n_{qi} =$										
15000	0.46	0.00	0.21	1373 \pm 140	297 \pm 72	290	1240	240	1450 \pm 110	315 \pm 105
20000	0.46	0.01	0.21	1528 \pm 160	339 \pm 81	339	1414	254	1668 \pm 123	368 \pm 117
30000	0.48	0.00	0.18	1852 \pm 189	410 \pm 101	400	1656	321	1986 \pm 144	437 \pm 138
40000	0.44	0.01	0.18	2102 \pm 197	440 \pm 103	453	1849	351	2210 \pm 166	483 \pm 159

Table 3. Mean size after harvest ($\bar{x} \pm \text{sd}$) and mean annual yield ($\bar{y} \pm \text{sd}$) during a period of 5,000 years of a moose population in relation to variation in the environmental stochasticity in calf survival (σ_{ep}) for proportional and threshold harvesting; $q_0 = 0.8$. For other parameters, see legend to Figure 1.

σ_{ep}	Proportional harvesting		Threshold harvesting	
	\bar{x}	\bar{y}	\bar{x}	\bar{y}
0.02	1644 \pm 152	347 \pm 81	1652 \pm 123	368 \pm 118
0.04	1528 \pm 160	339 \pm 81	1668 \pm 123	368 \pm 117
0.06	1511 \pm 161	332 \pm 79	1674 \pm 129	366 \pm 121

animals remaining after the hunt when the population was subject to proportional harvesting (Table 3). However, increasing the environmental variability had much less impact on the population when threshold harvesting was performed. A similar annual yield was maintained even though the variance in the annual yield still was higher than for proportional harvesting.

Discussion

Our study demonstrates that optimal harvesting of a moose population with respect to maximising the annual yield in terms of number of animals involves intense harvesting of calves and bulls, whereas the harvest rate of adult females should be very low (see Fig. 3). In general, threshold harvesting gives higher mean annual yields than proportional harvesting (see Fig. 4, and Tables 1, 2 and 3). In contrast, the variation among years in the annual yield is lower for proportional than for threshold harvesting (see Fig. 1, 2B and 4, and Tables 1, 2 and 3). These patterns remained also when optimising the mean annual yield of meat. The relative difference between the two harvesting strategies increased with reduced calf survival rate (see Fig. 3), increasing environmental stochasticity (see Table 3) and strength of density dependence in survival rates (see Table 2).

We have previously shown, using diffusion approximation to simple stochastic population models with density regulation, that threshold harvesting gives more sustained exploitation than proportional as well as constant harvest strategies (Lande, Engen & Sæther 1994, Lande et al. 1995, 1997, Sæther, Engen & Lande 1996b, Engen, Lande & Sæther 1997, see also Whittle & Horwood 1995). Our analysis of the harvest of moose supports this conclusion even in a far more complicated model involving age-structure, density dependence and demographic as well as environmental stochasticity in the population dynamics. This difference becomes larger with increasing environmental

stochasticity and strength of density regulation in the survival, and when the mean annual growth rate is reduced (see Tables 2 and 3, and Fig. 4). This illustrates that threshold harvesting represents a more sustainable exploitation strategy of populations in a fluctuating environment because there is no harvest in years with small population sizes. Furthermore, this also shows that analytical results obtained from very simplified models may provide insight into general processes and suggest management strategies that otherwise would have been difficult to obtain.

These analyses assume no bias in population estimates and precise estimates of population parameters. Some modified threshold harvesting often give higher mean annual yields than applying a pure proportional harvesting strategy (Engen et al. 1997, Tufto, Sæther, Engen, Swenson & Sandegren 1999, Aanes et al. in press). When including such uncertainties in the analysis, the differences between the two harvest strategies may also be larger. Accordingly, Luoma, Ranta & Kaitala (2001) found a large effect of bias in population estimates on the choice of harvest strategy.

The high variance in the annual yield represents a problem with implementation of threshold harvesting strategies into practical moose management. One way to reduce the variance in the annual harvest may be to use nearly optimal harvest strategies. For instance, proportional threshold harvesting, i.e. harvesting only a fraction of the estimated population size above the threshold, reduces the variance in the yield (Engen et al. 1997). For high calf survival rates the difference in yield between the harvesting strategies was relatively small (see Fig. 4), suggesting that the choice of harvest strategies will be of minor importance. However, in some areas of Scandinavia we now experience an increase in the population size of large predators such as the brown bear *Ursus arctos* (e.g. Swenson, Sandegren, Bjärvall, Söderberg, Wabakken & Franzén 1994) and the wolf *Canis lupus* (P. Wabakken, unpubl. data). If this results in a decrease in the natural survival rate of moose calves (e.g. Larsen, Gauthier & Markel 1989, Ballard, Whitman & Reed 1991), this reduction will result in a larger difference in the mean annual yield between threshold and proportional harvesting (see Fig. 4). Thus, we suggest that a shift should occur from proportional to threshold harvesting in areas where dense populations of large predators are expected to appear in the future.

Optimal harvest of a moose population involves, whatever choice of harvest strategy, high harvest rates of calves and bulls, and a small offtake of adult females (see Fig. 3 and Table 1). Such an age- and sex-biased

harvest strategy is in accordance with the results from analyses of deterministic age-specific harvest models (Caughley 1977, Cederlund & Sand 1991, Sæther, Solbraa, Sødal & Hjeljord 1992, Getz & Haight 1989, Sylven 1995), where changes in the sex-composition of the quota are considered as the most important tool for increasing the yield of populations of relatively long-lived species (see Haagenrud et al. 1987 and Nygren & Pesonen 1993 for a description of a practical application of this strategy for moose in Fennoscandia). However, this requires that a small number of bulls are able to impregnate a large proportion of the fertile females in the populations (Caughley 1977, Ginsberg & Milner-Gulland 1994, Langvatn & Loison 1999). We have chosen a relatively modest effect of variation in the sex ratio on the probability of conception. For instance, we assume that 90% of the females conceived when the sex ratio s is 33% (see Model section). If the sex ratio is reduced to 25%, the probability of conceiving is 0.82. This neglects any unfortunate consequences of a biased sex ratio in the population. A stronger constraint on the sex ratio in the population reduces the yield and requires a larger harvest of calves (see Table 1).

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